

Paleoecology and paleoenvironments of the Pleistocene deposits of Bahia la Choya (Gulf of California, Sonora, Mexico)

By

MARTIN ABERHAN & FRANZ T. FÜRSICH *)

With 15 figures in the text and 4 plates

ABSTRACT

Late Pleistocene (Sangamonian) sediments in the vicinity of Bahia la Choya consist of shell-rich, in places cobbly, fine- to coarse-grained sandstones. The rich benthic macrofauna is represented by 115 species with bivalves being the most diverse and most abundant group. Taphonomic data suggest that shell concentrations formed either by low rates of net sedimentation, by storms, or, most commonly, by a combination of both. Five recurrent associations (*Chione* A, *Chione* B,

Ostrea-Chione, *Donax-Felaniella*, and balanid-vermetid) are recognized which apparently underwent differing degrees of time-averaging. The associations exhibit a good correlation with parameters of the substrate such as grain size and substrate consistency. Based on taphonomic, ecologic, and sedimentological criteria, the depositional environment of the Pleistocene ranged from the very shallow sandy subtidal to the rocky intertidal.

KURZFASSUNG

Spätpleistozäne Sedimente in der Umrandung von Bahia la Choya, einer Bucht am Nordostrand des Golfs von Kalifornien, bestehen aus schillreichen, fein- bis grobkörnigen Sandsteinen, die an manchen Lokalitäten zahlreiche gerundete Blöcke enthalten. Die benthonische Makrofauna besteht aus 115 Arten, wobei Muscheln die arten- und individuenreichste Gruppe sind. Die taphonomische Analyse ergab, daß die Schillagen teils durch eine niedrige Nettosedimentationsrate, teils durch Stürme gebildet wurden, am häufigsten jedoch durch eine Kombination beider Faktoren. Die palökologische Analyse der Fauna ergab fünf Assoziationen (*Chione* A, *Chione* B, *Donax-Felaniella*, *Ostrea-Chione* und Balaniden-

Vermetiden). Die zum Teil erheblichen Schwankungen der Diversitätswerte innerhalb einzelner Assoziationen dürften auf Unterschiede in der zeitlichen Mittelung der Faunen zurückzuführen sein. Die Assoziationen zeigen eine gute Korrelation mit Eigenschaften des Substrats, vor allem der Korngröße und der Festigkeit. Aufgrund sedimentologischer, taphonomischer und ökologischer Kriterien sowie durch einen Vergleich mit heutigen Milieus von Bahia la Choya läßt sich das Ablagerungsmilieu des Pleistozäns gut eingrenzen. Es reichte vom sehr flachen, sandigen Subtidal bis zum geröllführenden Intertidal.

INTRODUCTION

Along the shores of the Gulf of California, Pleistocene (Sangamonian) rocks, representing shallow water deposits, occur at various localities (e. g. DURHAM 1950, HERTLEIN 1957, HERTLEIN & EMERSON 1959, EMERSON 1960, EMERSON & HERTLEIN 1964, STUMP 1975, 1981, BECKVAR & KIDWELL 1988). Due to their young age and mollusc fauna, which is very similar to

that of present-day nearshore environments, they are ideal objects for paleoecological analysis. One of these occurrences are the rocks fringing the small embayment of Bahia la Choya, north of Puerto Peñasco (Fig. 1). Although easily accessible and very fossiliferous, the rocks have been little studied in the past. The aim of the present study is to describe these Pleistocene rocks in detail, to record the benthic macrofauna, analyse its taphonomic history and paleoecology, and reconstruct the depositional environments.

* M. ABERHAN, F. T. FÜRSICH, Institut für Paläontologie der Universität, Pleicherwall 1, W-8700 Würzburg, Germany.

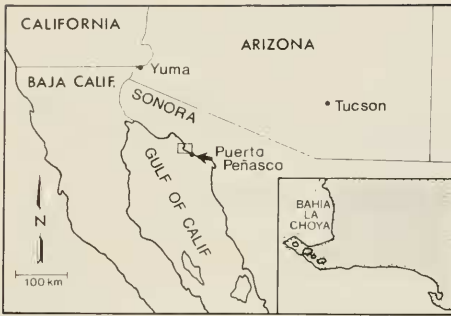


Fig. 1: Locality map.

Bahia la Choya is a macrotidal system with a spring tidal range of 7.9 m (THOMSON et al. 1969). Due to very low rates of net sedimentation, patches of Pleistocene rocks occur on the tidal flat and in very shallow subtidal areas. More prominently, Pleistocene rocks form a high intertidal terraced platform in the northern part of the bay. Smaller outcrops occur along the southern, rocky shore of Bahia la Choya, where Pleistocene sediments often form a thin veneer on top of, or occupy pockets between, crystalline rocks. More extensive sections occur near Pelican Point (Fig. 2, locality 6). Small, isolated outcrops also exist in the tidal channel of the flat and along the southern bank of the channel in the salt marsh.

METHODS

Six sections, varying between 1 and 7 m in thickness were measured in the immediate vicinity of the bay (Fig. 2). Lateral variations in thickness, bed contacts, grain size, mineralogical composition, and sedimentary structures were recorded. In addition, observations on bioturbation, biofabric, and percentage of articulated shells were made. Sixteen fossiliferous bulk samples were taken back to the laboratory and mechanically disaggregated to obtain the macrofauna. This fauna was identified using KEEN (1971), KEEN & COAN (1976), and BRUSCA (1980). For each species, the following data were recorded:

- number of right and left valves,
- number of articulated specimens,

The Pleistocene rocks consist of strongly to poorly cemented, fine- to coarse-grained sandstones and conglomerates. Shells and shell fragments, predominantly of molluscan origin, constitute an important part of the sediment and frequently form skeletal concentrations. This fauna was first mentioned and identified by HERTLEIN & EMERSON (1956) who listed 33 species of bivalves and 26 species of gastropods. Based on the great similarity of the fossil fauna of Bahia la Choya to that of other Pleistocene localities as well as to that of Recent shallow subtidal and intertidal faunas, HERTLEIN & EMERSON (1956) assumed a Late Pleistocene age of the terraces (see also STUMP 1981). Radiometric dating of rocks in comparable stratigraphic positions along the Sonoran coast yielded ages between 80,000 and 120,000 years (BERNAT et al. 1980, ORTLIEB 1982, 1984a). This implies that the deposits formed during the last interglacial stage (Sangamonian) when the mean sea level was up to 9 m higher than at present times (ORTLIEB 1984b).

Taphonomic studies have been carried out on shell beds in the Pleistocene terrace of Punta Chueca (BECKVAR & KIDWELL 1988) and STUMP (1975) analysed the paleoecology of mollusc assemblages of the Puerto Libertad region. Based on a brief comparison of the Puerto Libertad fauna and that of two other localities with the fauna of the Bahia la Choya Pleistocene, STUMP (1981) interpreted the Bahia la Choya deposits as having formed in sandy to hard substrates of the intertidal and subtidal.

- number of bored and encrusted specimens,
- diversity (number of species) and taxonomic composition of encrusters and borers,
- preservation quality,
- maximum size, and
- number and size of internal moulds.

Fragments counted as one individual, if the hinge (in the case of bivalves) or more than half the shell (in the case of gastropods) was preserved.

Acetate peels and thin sections of each sample provided information on biofabric, grain size distribution, sorting, shell density and the diagenetic history of the Pleistocene rocks.

LITHOFACIES

Six sections, ranging from 0.4 to 7.0 m in thickness, were measured and sampled (Fig. 2). The sediments consist of fossiliferous, strongly to poorly cemented, fine to coarse-grained sandstones and conglomerates. They rest unconformably on Mid-Tertiary(?) granites or basalts. Due to a high rate of bioturbation and a generally low rate of net sedimentation, sedimentary structures are rare. Lithofacies vary laterally between sections (Fig. 2). Sections 5 and 6 typically contain abundant pebbles and cobbles up to 50 cm in diameter, whereas

sections 1, 2, 3 and 4 have few pebbles and cobbles and are generally better sorted.

The most conspicuous feature of the sediments are the skeletal concentrations (e. g. Pl. 1, Figs 2-3). The degree of packing ranges from bioclast-supported (e. g. Pl. 2, Fig. 1) to matrix-supported. Shells are usually well preserved but in some cases small, thin, and/or aragonitic shells are preferentially dissolved and are now represented by casts and molds.

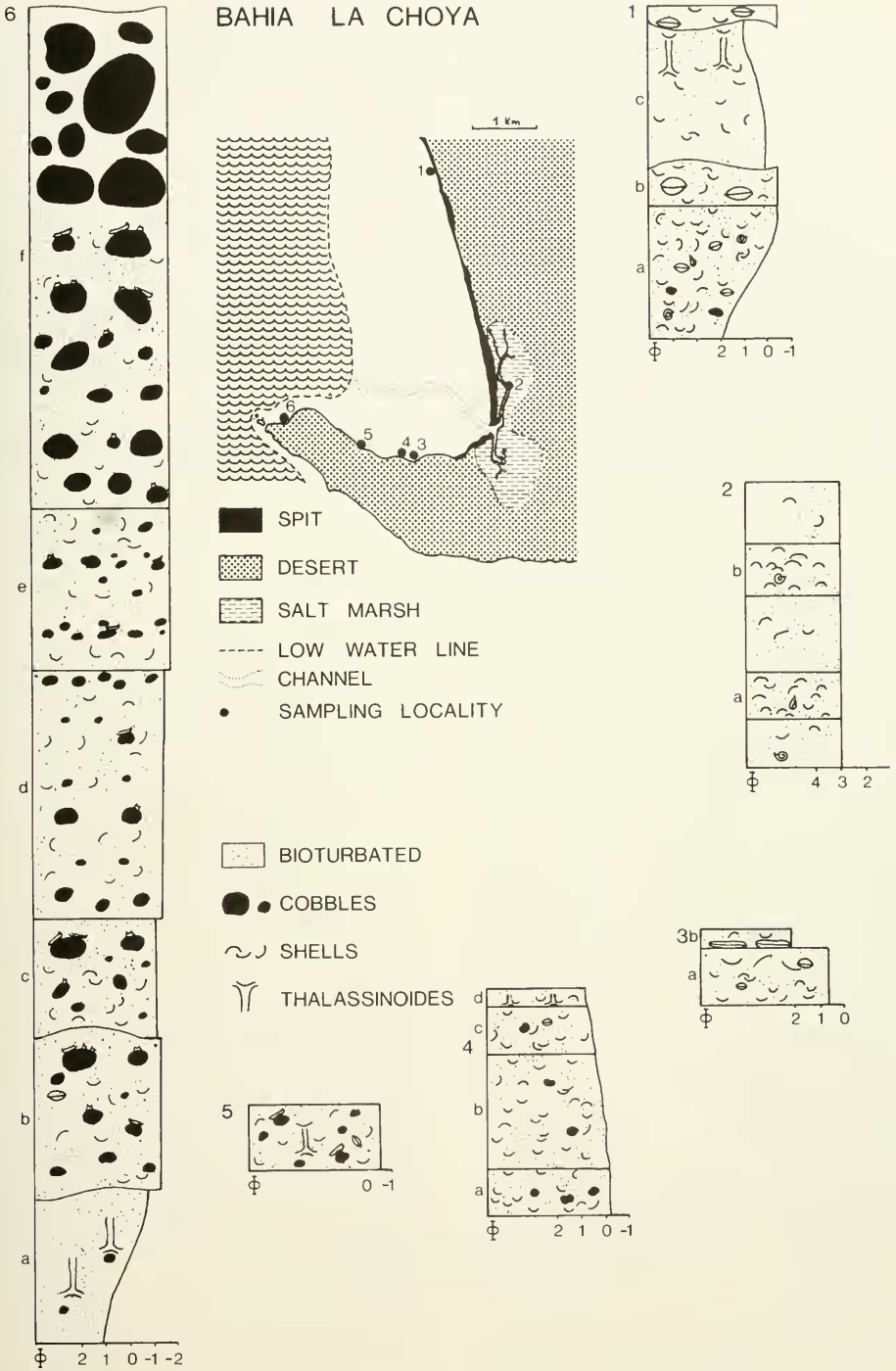


Fig. 2: Sampling localities (1-6) and sections of Pleistocene rocks in the vicinity of Bahia La Choya.

The highly diverse benthic fauna is dominated by bivalves and gastropods. At one locality barnacles are the most abundant faunal element. Most bivalves are oriented convex-down or oblique. In some layers articulated shells are common.

Cryptocrystalline micrite cement is responsible for cemen-

tation. Furthermore fibrous and fine-granular cement A are common on micritized shells (Pl. 2, Fig. 5). Dog-tooth cement is rare. Most of the carbonate and non-carbonate components have micrite envelopes. Recrystallisation of shell material is common (Pl. 2, Fig. 4).

FAUNAL COMPOSITION

More than 4600 specimens were collected, representing 115 species of marine invertebrates (62 species of bivalves, 49 species of gastropods, 2 species of barnacles, 1 scaphopod and 1 echinoid). Bivalves are by far the most abundant group. Table 1 lists all species in systematic order together with information on life habits, feeding habits, and substrate preferences. 55.4% of the species are infaunal, 44.6% are epifaunal. Most of the species are suspension-feeders (56.3%), fol-

lowed by carnivores (20.5%), detritus-feeders (13.4%) and herbivores (9.0%). 65.2% prefer soft substrate, 33.9% occur in or on hard substrate.

All of the identified species occur in shallow subtidal and intertidal environments of Bahía la Choya today. Most are adapted to strong fluctuations of environmental parameters, such as temperature, salinity, and oxygen content.

Table 1: List of species encountered in Pleistocene rocks at Bahía la Choya with information on life habits, feeding habits, and substrate preferences of species. — EC: epifaunal cemented; EB: epibyssate; EF: epifaunal free living; IS shallow infaunal; ID: deep infaunal; trophic groups: D: deposit-feeder; S: suspension-feeder; H: herbivore; C: carnivore; substrate: s: soft; h: hard.

BIVALVIA	LIFE HABIT	TROPHIC GROUP	SUBSTRATE		LIFE HABIT	TROPHIC GROUP	SUBSTRATE
<i>Nucula (Nucula) declivis</i> HINDS 1843	IS	D	s	<i>Orobitella obliqua</i> (HARRY 1969)			
<i>Arca (Arca) mutabilis</i> (SOWERBY 1833)	EB	S	h	<i>Chama</i> sp.	EC	S	h
<i>Barbatia (Calloarca) alternata</i> (SOWERBY 1833)	EB	S	h	<i>Trachycardium (Mexicardia) panamense</i> (SOWERBY 1833)	IS	S	s
<i>B. (Fugleria) illata</i> (SOWERBY 1833)	EB	S	h	<i>Trigoniocardia (Trigoniocardia) granifera</i> (BRODERIP & SOWERBY 1829)	IS	S	s
<i>Anadara (Larkinia) multicosata</i> (SOWERBY 1833)	EB	S	s	<i>Laevicardium elatum</i> (SOWERBY 1833)	IS	S	s
<i>Arcopsis solida</i> (SOWERBY 1833)	EB	S	h	<i>L. etenense</i> (SOWERBY 1840)	IS	S	s
<i>Glycymeris (Glycymeris) gigantea</i> (REEVE 1843)	IS	S	s	<i>Tivela (Tivela) byronensis</i> (GRAY 1838)	IS	S	s
<i>G. (Tucetona) multicosata</i> (SOWERBY 1833)	IS	S	s	<i>Pitar (Pitar) helenae</i> OLSSON 1961	IS	S	s
<i>Brachidontes semilaevis</i> (MENKE 1849)	IS	S	h	<i>Megapitaria squalida</i> (SOWERBY 1835)	IS	S	s
<i>Lithophaga (Labis) sp.</i>	IS	S	h	<i>Dosinia dunkeri</i> (PHILIPPI 1844)	IS	S	s
<i>Modiolus capax</i> (CONRAD 1837)	EB	S	h	<i>D. ponderosa</i> (GRAY 1838)	IS	S	s
<i>Atrina</i> sp.	IS	S	s	<i>Chione (Chione) californienses</i> (BRODERIP 1835)	IS	S	s
<i>Pteria sterna</i> (GOULD 1851)	EB	S	h	<i>C. (Chionista) fluctifraga</i> (SOWERBY 1853)	IS	S	s
<i>Ostrea</i> sp.	EC	S	h	<i>C. (Chionopsis) gnidia</i> (BRODERIP & SOWERBY 1829)	IS	S	s
<i>Pecten (Oppenheimopecten) vogdesi</i> ARNOLD 1906	EF	S	s	<i>C. (C.) pulicaria</i> (BRODERIP 1835)	IS	S	s
<i>Argopecten circularis</i> (SOWERBY 1835)	EF	S	h	<i>C. (Lirophora) mariae</i> (D'ORBIGNY 1846)	IS	S	s
<i>Anomia adamas</i> GRAY 1850	EB	S	h	<i>Protothaca (Tropithaca) grata</i> (SAY 1831)	IS	S	s
<i>Cardita (Byssamera) affinis</i> SOWERBY 1833	EB	S	h	<i>Macra (Macrotoma) nasuta</i> GOULD 1851	IS	S	s
<i>Lucina (Callucina) lampra</i> (DALL 1901)	ID	S	s	<i>M. (Micromacra) californica</i> CONRAD 1837	IS	S	s
<i>Parvilucina (Parvilucina) mazatlanica</i> (CARPENTER 1855)	ID	S	s	<i>Raeta undulata</i> (GOULD 1851)	IS	S	s
<i>P. (Cavilinga) prolongata</i> (CARPENTER 1857)	ID	S	s	<i>Tellina (Angulus) meropsis</i> DALL 1900	ID	D	s
<i>Ctena mexicana</i> (DALL 1901)	ID	S	s	<i>T. (Eurytellina) simulans</i> C. B. ADAMS 1852	ID	D	s
<i>Diplodontia orbella</i> (GOULD 1852)	IS	S	s				
<i>Felaniella (Zemysia) sericata</i> (REEVE 1850)	ID	S	s				

	LIFE HABIT	TROPHIC GROUP	SUB- STRATE		LIFE HABIT	TROPHIC GROUP	SUB- STRATE
<i>T. (Lacialina) ochracea</i> CARPENTER 1864	ID	D	s	<i>Crepidula striolata</i> MENCKE 1851	EF	S	h
<i>Leporimetis (Florimetis) cognata</i> (PILSBRY & VANATTA 1902)	ID	D	s	<i>Crucibulum (Crucibulum) scutellatum</i> (WOOD 1828)	EF	S	h
<i>Strigilla (Pisostrigilla) interrupta</i> MOERCH 1860	ID	D	s	<i>C. (C.) spinosum</i> (SOWERBY 1824)	EF	S	h
<i>Tellidora burneti</i> (BRODERIP & SOWERBY 1829)	ID	D	s	<i>Natica (Natica) chemnitzii</i> PFEIFFER 1840	IS	C	s
<i>Donax gracilis</i> HANLEY 1845	IS	S	s	<i>Polinices (Polinices) uber</i> (VALENCIENNES 1832)	IS	C	s
<i>D. navicula</i> HANLEY 1845	IS	S	s	SCAPHOPODA			
<i>Heterodonax pacificus</i> (CONRAD 1837)	IS	S	s	<i>Dentalium</i> sp.	IS	D	s
<i>Tagelus (Tagelus) sp.</i>	ID	S	s	ECHINOIDEA			
<i>Semele flavescens</i> (GOULD 1851)	ID	D	s	<i>Encope</i> sp.	IS	D	s
<i>S. javis</i> (REEVE 1853)	ID	D	s	<i>Neveria (Glossaulax) reclusiana</i> (DESHAYES 1839)	IS	C	s
<i>Solen (Solen) rosaceus</i> CARPENTER 1864	IS	S	s	<i>Cymatium (Turrition) gibbosum</i> (BRODERIP 1833)	EF	C	h
<i>Cryptomya californica</i> (CONRAD 1837)	ID	S	s	<i>Hexaplex erythrostomus</i> (SWAINSON 1831)	EF	C	h
<i>Corbula (Caryacorbula) marmorata</i> HINDS 1843	IS	S	s	<i>Acanthina angelica</i> OLDROYD 1918	EF	C	h
<i>C. (Juliacorbula) bicarinata</i> SOWERBY 1833	IS	S	s	<i>Neorapana tuberculata</i> (SOWERBY 1835)	EF	C	h
<i>C. (J.) biradiata</i> SOWERBY 1833	IS	S	s	<i>Solenosteira macrospira</i> BERRY 1957	EF	C	h
<i>Cyathodonta</i> sp.				<i>Columbella</i> sp.	EF	S	h
GASTROPODA				<i>Anachis</i> sp.	EF	D	h
<i>Diodora inaequalis</i> (SOWERBY 1835)	EF	H	h	<i>Melongena patula</i> (BRODERIP & SOWERBY 1829)	EF	C	s
<i>Collisella stanfordiana</i> (BERRY 1957)	EF	H	h	<i>Nassarius (Nassarius) versicolor</i> (C. B. ADAMS 1852)	EF	C	s
<i>Tegula (Agathistoma) felipensis</i> MCLEAN 1970	EF	H	h	<i>N. (Phrontis) iodes</i> (DALL 1917)	EF	C	s
<i>T. (A.) mariana</i> DALL 1919	EF	H	h	<i>N. (Phrontis) brunneostoma</i> (STEARNS 1893)	EF	C	s
<i>T. (Chlorostoma) rugosa</i> (A. ADAMS 1853)	EF	H	h	<i>Fusinus</i> sp.	EF	C	s
<i>Turbo (Callopora) fluctuosus</i> WOOD 1828	EF	H	h	<i>Oliva (Oliva) incrassata</i> (LIGHTFOOD 1786)	IS	C	s
<i>Nerita (Thelastyla) funiculata</i> MENKE 1851	EF	H	h	<i>O. (O.) spicata</i> (ROEDDING 1798)	IS	C	s
<i>Theodoxus (Vitocliton) luteofasciatus</i> MILLER 1879	EF	H	h	<i>Agaronia testacea</i> (LAMARCK 1811)	IS	C	s
<i>Turritella anactor</i> BERRY 1957	IS	S	s	<i>Olivella (Olivella) dama</i> (WOOD 1928 ex MAWE, MS)	IS	C	s
<i>T. leucostoma</i> VALENCIENNES 1832	IS	S	s	<i>Canus (Lepteconus) regularis</i> SOWERBY 1833	EF	C	s
<i>Modolus disculus</i> (PHILIPPI 1846)	EF	?	h	<i>C. (Ximeniconus) perplexus</i> SOWERBY 1857	EF	C	s
<i>Vermetus (Thylaeodus) indentatus</i> (CARPENTER 1857)	EC	S	h	<i>Terebra armillata</i> HINDS 1844	IS	C	s
<i>Tripsycha (Eualetes) centiquadra</i> (VALENCIENNES 1846)	EC	S	h	<i>T. elata</i> HINDS 1844	IS	C	s
<i>Dendropoma lituella</i> (MOERCH 1861)	EC	S	h	<i>Pyramidella</i> sp.	EF	C	s
<i>Cerithium (Thericium) stercusmuscarum</i> VALENCIENNES 1833	EF	H	h	<i>Bulla (Bulla) gouldiana</i> PILSBRY 1895	IS	C	s
<i>Cerithidea mazatlanica</i> CARPENTER 1857	EF	D	s	<i>Acteocina inculta</i> (GOULD & CARPENTER 1857)	IS	C	s
<i>Rhinocoryne humboldtii</i> (VALENCIENNES 1832)	EF	D	s	<i>Melampus (Melampus) mousleyi</i> BERRY 1964	EF	H	s
<i>Hipponix panamensis</i> C. B. ADAMS 1852	EF	S	h	CIRRIPEDIA			
<i>Calyptraea (Calyptraea) mamillaris</i> BRODERIP 1834	EF	S	h	<i>Balanus improvisus</i> DARWIN 1854	EC	S	h
				<i>Tetraclita</i> sp.	EC	S	h

TAPHONOMY

MODES OF SHELL BED FORMATION

The taphonomic features of skeletal concentrations are a powerful tool for deciphering their mode of formation (e. g. KIDWELL et al. 1986). In this study, taphonomic parameters such as right/left valve ratio of bivalves, degree of articulation, abrasion and fragmentation, encrustation, bioerosion, chemical dissolution, orientation, shell density and maximum size of shells within the various species are used to distinguish three modes of shell bed formation. Table 2 summarizes the expected taphonomic features ("taphofacies" sensu SPEYER & BRETT 1986) of shell concentrations formed by

- (a) short-term events (e. g. storms).
- (b) long-term wave and current action, and
- (c) omission.

Table 2: Taphonomic features of shell beds formed by three different modes.

taphonomic parameters	concentration of shells by		
	short term events (storms)	long term wave and current action	omission
percentage of articulation	high - medium	low	low
right-left valve ratio	≈ 1	$\neq 1$	$\neq 1$
abrasion and breakage	medium - low	high	low
bioerosion and encrustation	low	medium	high
orientation		convex up	

Shell beds formed by short-term events

Recognition of the importance of short-term, "catastrophic" events for stratigraphy (AGER 1973, SEILACHER 1982, DOTT 1983) led to better understanding of the formation of storm deposits. Most storm deposits have been recognized by a characteristic succession of sedimentological features (BRENNER & DAVIES 1973, KELLING & MULLIN 1975, BRENCHLEY et al. 1979, KREISA 1981, KREISA & BAMBACH 1982, AIGNER 1982). In sequences lacking physical sedimentary structures, as is the case in the Pleistocene sediments of Bahía la Choya, the influence of storms in shell bed formation cannot be assessed with lithological criteria alone. BECKVAR (1986) used taphonomic criteria to distinguish between skeletal concentrations formed by storms and those formed by low rates of net sedimentation (degree of articulation of bivalves and level of encrustation of shells).

During storms, shells of living and dead organisms are exhumed and immediately redeposited. Fast burial by sediment deposited out of suspension during the waning stages of the storm event protects the majority of shells from destructive processes on the sea floor. Therefore, the following taphonomic features can be expected of skeletal concentrations formed by storms (disregarding the effects of earlier, pre-storm processes):

- a high to medium percentage of articulated shells;
- roughly equal numbers of right and left valves;
- a low to medium level of abrasion and breakage;
- a low degree of bioerosion and encrustation, and
- a bioclast-supported fabric produced by winnowing. In a complete sequence shell density decreases from bottom to top.

The orientation of shells, which depends on the energy level during time of deposition, is less diagnostic of storm sedimentation. For example, bottom return flows will arrange shells preferentially in a convex-up position (e. g. BRENNER & DAVIES 1973). In contrast, deposition of suspended shells below the zone of turbulence during waning stages of the storm produces a predominantly convex-down valve pattern (e. g. AIGNER 1982).

Shell beds formed by long-term wave and current action

Long-term exposure to wave and current action imply a higher energy level and a dominance of physical processes such as transport and/or frequent reworking. The following features can be expected:

- a low degree of articulation;
- strongly differing numbers of right and left valves;
- a high degree of sorting according to weight, shape, and/or size;
- a high level of abrasion and breakage;
- a medium level of bioerosion and encrustation, and
- a preferentially convex-up position in the case of currents.

Shell beds formed by omission

Omission (either caused by starvation or by-passing) or a low rate of net sedimentation imply long exposure times and a slow burial of shells on the sea floor. The following taphonomic features of skeletal concentrations formed by omission or a low rate of net sedimentation can be expected:

- a low percentage of articulation;
- a corresponding number of right and left valves (as long as extensive transport is not involved);
- a low degree of abrasion and breakage;
- a high level of bioerosion and encrustation, and
- a high shell density.

Omission and reduced sedimentation does not produce a characteristic orientation. The latter depends on the influence of currents and waves and on the degree of post-depositional physical and biological reworking.

In the following, the Pleistocene shell concentrations of Bahía la Choya are analysed according to these criteria.

Table 3: Right-left valve ratio of six common bivalves. Numbers in brackets refer to numbers of individuals. 1a-6c: samples from the Pleistocene; R: sample from taphocoenosis of the Recent shallow subtidal.

	<i>Chione californiensis</i>	<i>Trachycardium panamense</i>	<i>Felaniella sericata</i>	<i>Donax navicula</i>	<i>Ostrea</i> sp.	<i>Lucina lampra</i>
1a	1.0 (847)					
1b	1.0 (147)	1.0 (64)				
1c	1.7 (153)	1.0 (53)	1.0 (122)	1.3 (87)		
2a			1.0 (56)	0.7 (65)		
2b			1.0 (98)	1.4 (85)		
3a	1.1 (247)					
3b	1.3 (172)					
4a	1.3 (255)					
4b	0.9 (40)					
4c	1.2 (50)					
5	1.6 (45)				1.6 (89)	
6b	1.2 (102)					
6c	1.1 (70)					
6d					1.8 (154)	
6e					0.5 (53)	
R	1.0 (156)		1.1 (157)	0.9 (46)		0.9 (348)

BAHIA LA CHOYA SHELL BEDS

The taphonomic features of the 16 Pleistocene samples are summarized in Table 3 and Figs 3-5. According to their mode of formation, shell beds can be assigned to one of three groups:

(a) Storm beds

Samples 1a-c and 4c belong to this group. On the whole, shells are well preserved. The percentage of bored and en-

crusted shells is low as are the degree of abrasion and breakage. The right/left valve ratio is close to 1. The percentage of articulated bivalves is medium to low. In some beds, particularly large individuals are still articulated (e. g. Pl. 1, Fig. 3). No shells were found in life position. Shells are oriented preferentially convex-down. Shell density is high.

Discussion. - The taphonomic features described here clearly reflect a short exposure time on the sea floor for most of the shells. Apparently there was not enough time for

Percentage of bored shells

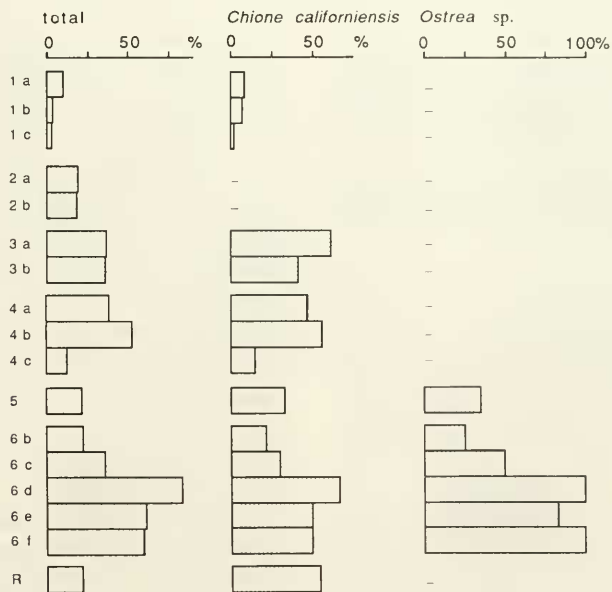


Fig. 3: Percentage of bored shells in the Pleistocene samples (1a-6f) and in a taphocoenosis from the Recent shallow subtidal (R).

boring and encrusting organisms to colonize skeletal hard-parts. Good preservation, especially of articulated bivalves, and the lack of shells in life position indicate exhumation and rapid burial of living organisms. The shell orientation pattern is characteristic of most of the Pleistocene deposits around Bahía la Choya. Processes, that may have contributed to the preferentially convex-down orientation of shells are

- lifting of valves by storms and subsequent settling below the zone of turbulent water;
- flipping over of convex-up oriented shells into a convex-down position by migrating sand ripples (CLIFTON 1971), or
- rotation of shells into a convex-down position by bioturbation (CLIFTON 1971).

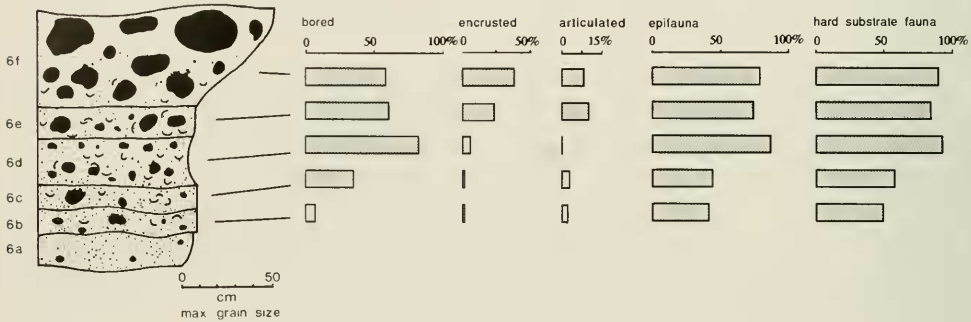


Fig. 4: Section through Pleistocene at locality 6 with taphonomic and ecologic data.

Post-mortem transport of shells was not significant as is indicated by a right/left valve ratio close to 1, a low percentage of fragmented shells, and the typical convex-down position of shells.

In summary, shells primarily were concentrated by short-term events, i. e. storms. Reworking by waves and organisms only played a limited role.

(b) Condensed beds

Samples 4 a and 4 b belong to this group. Due to a high percentage of bored shells (for types of borings see Pl. 3, Figs 2, 5–7), shell material is generally fairly worn. No shells are encrusted. Shell fragments are common. Roughly the same number of right and left valves was found. No articulated bivalves were present. Shells are preferentially oriented convex-down.

Discussion. – The high percentage of bored shells, absence of articulated bivalves, and occurrence of fragmented shells show, that skeletal hard-parts were lying on the sea floor for a considerable period of time, indicating low rates of sedimentation. As a result extensive biological and physical reworking occurred. The influence of storms is difficult to assess, as no features diagnostic of storms are preserved. Trans-

The high percentage of vertical and/or obliquely oriented valves can be the result of bioturbation (SALAZAR-JIMÉNEZ et al. 1982) or of high energy conditions in very shallow water.

The contribution of each of these processes is difficult to assess, because physical and biogenic sedimentary structures are rarely preserved.

The percentage of articulated bivalves in the Pleistocene shell beds is lower than would be expected in storm deposits. This could be a result of physical and/or biological reworking prior to and/or after major storm events. Apparently, wave action and burrowing organisms caused separation of valves in layers a and c of locality 1. Reworking was not strong enough, however, to affect the large articulated individuals of layers 1b and 4c.

port of shell material was insignificant for the same reasons as discussed under (a).

(c) Mixed origin beds

In mixed origin beds skeletal concentrations were formed by the interplay of two or more kinds of processes, or by the strong overprinting of a precursor concentration of one type by later processes of a different kind (KIDWELL et al. 1986). Samples 2 a–b and 3 a–b can be assigned to this group.

Samples 2 a–b are characterized by a low to medium percentage of bored shells. No shells are encrusted. The degree of abrasion and breakage is moderate. The percentage of articulated bivalves is low. Some bivalves were found in life position. The right-left valve ratio is close to 1. Shells are oriented preferentially convex-up. In both samples small and large individuals are present; however, shells of the same species clearly are larger in 2b (Pl. 3, Fig. 1).

Samples 3 a–b are characterized by a medium to high level of bioerosion. The degree of breakage is low. A relatively high percentage of bivalves is articulated. No fossils were found in life position. The number of unbroken shells and articulated bivalves decreases from bottom to top. The right-left valve ratio is close to 1. Most valves are oriented convex-down.

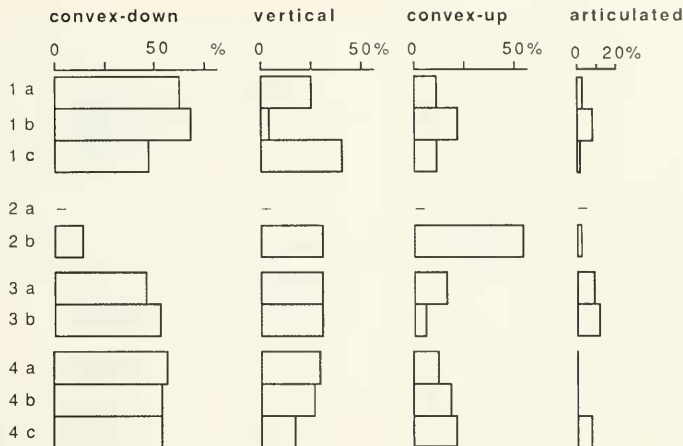


Fig. 5: Orientation and percentage of articulation of shells at localities 1-4.

Discussion. — In 2a and 2b the presence of articulated shells, albeit in low numbers, suggests exhumation of live individuals by storms and rapid redeposition during the waning stages. Low to medium levels of abrasion, fragmentation, bioerosion and encrustation support this interpretation. The orientation pattern differs from the rest of the Pleistocene samples. The hydrodynamically stable convex-up position of most shells is a good indicator for the influence of currents during the time of deposition. Thus, limited transport may have contributed to the concentration of shells. Long distance transport however is not likely to have occurred, as indicated by the right-left valve ratio and relatively low levels of abrasion and fragmentation. Reworking was limited as is suggested by the presence of some articulated shells. The occurrence of larger shells of the same species in 2b may have its origin in different ecological conditions (higher environmental stress in 2a) or a different hydrodynamic system (higher water energy in 2b was able to transport larger shells over short distances). On the whole, shell beds 2a and 2b can be regarded as the result of the interplay of storm processes and current action. Currents in shallow marine environments such as Bahía la Choya today and during Pleistocene times can be induced by tides, especially in channels, by bottom return flows during storm action, and by long-shore currents.

In 3a and 3b the relatively high percentage of articulated bivalves (none of them in life position) again suggests storm influence. However the relatively high percentage of bored individuals demonstrates, that many shells were lying on the sea floor for a considerable period of time indicating low rates of net sedimentation. The high number of broken shells and disarticulated bivalves in the upper part of layers 3a and 3b demonstrate, that subsequent reworking modified these parts of the shell beds. Thus these shell beds show the characteristic taphonomic features of both storm beds and condensed beds. Lateral transport does not seem to have played an important role, as is indicated by a relatively high degree of articulation, a common convex-down position, and a right-left valve ratio close to 1.

Due to limited outcrop area and ambiguous taphonomic data, sample 5 cannot be assigned to any of the modes of shell bed formation discussed above.

REGRESSIVE TRENDS DEDUCED FROM TAPHONOMIC DATA

We have not yet considered the samples of locality 6. These come from the thickest section (7 m), and they provide an opportunity to analyse the depositional environment by studying trends of taphonomic parameters through time (Fig. 4).

Sample 6a consists of densely-packed shell fragments. Preparation and identification of fossils was not possible. The absence of articulated bivalves and a very high level of fragmentation is the only available taphonomic information.

From layers 6b-f, the degree of boring, encrustation, articulation and fragmentation generally increases from bottom to top. It is only here that encrusting organisms such as balanids, vermetids, bryozoans, serpulids, and spirorbids reach considerable abundance and diversity. The vast majority of encrusters (for characteristic species see Pl. 1, Fig. 5, Pl. 2, Fig. 3, Pl. 3, Figs 3-4) colonised epifaunal species. In 6b and 6c, the right-left valve ratio is close to 1, in 6d and 6e it clearly differs from 1. In 6f none of the bivalves was abundant enough to provide significant information.

Discussion. — In sample 6a the absence of articulated bivalves and a high level of fragmentation suggest a high energy level and frequent reworking.

From 6b-f, an increasing level of bioerosion and encrustation points to increasing residence time of shells resulting from decreasing rates of sedimentation.

The increasing percentage of fragmented shells suggests an increase in the energy level. The increasing disparity between right and left valves indicates increasing importance of long-term wave and current action. Apart from mechanical sorting, however, sorting caused by bioerosion also occurred. In

sample 6f for instance, the cemented bivalve *Chama* sp. is represented by 12 thick-shelled, sturdy left valves, but only 1 thinner-shelled right valve. All valves are heavily bored and, due to diagenetic alteration, are very chalky (Pl. 3, Fig. 3). Most likely, some of the less preservable right valves were destroyed by bioerosion.

The relatively high percentage of articulated shells toward the top (6e-f) appears to contradict the increase in water energy postulated by other taphonomic features. This anomaly can be explained by the protection of epifaunal and infaunal organisms offered by the increasing number of large cobbles toward the top (Pl. 1, Fig. 4).

In summary, residence time of shells on the substrate increased toward the top, as did the wave and current action. The energy level increased, whereas sedimentation rates decreased. These trends are best interpreted as a result of shallowing of the depositional environment. This assumption is corroborated by the coarsening upward sedimentary sequence which also implies shallowing in a steep, high energy coastal environment. Taphonomic data thus not only contribute to decipher the mode of formation of skeletal concentrations, but also provide useful information on bathymetry and regressive/transgressive gradients in the history of depositional environments.

FOSSIL DIAGENESIS

A study of the diagenetic features of shells from the 16 samples showed that chemical degradation of shells depended on size, mineralogy, shell microstructure, and the surface area to weight ratio of the hard-parts. Within the same species shells of gastropods show the strongest traces of dissolution, followed by aragonitic bivalves (e.g. *Chione*, *Trachycardium*, *Donax*). Shells with purely or predominantly calcitic material are always preserved with the original shell material (e.g. *Ostrea*, *Chama*, balanids, bryozoans). Shells with a high sur-

face area to weight ratio such as *Tagelus* and *Felaniella* were preferentially dissolved.

Typical patterns of hard-part dissolution are the development of a chalky surface (Pl. 4, Figs 1, 4), the thinning of the distal margins (Pl. 4, Fig. 3), the accentuation of pre-existing shell sculpture (Pl. 4, Fig. 3), and the preferential dissolution of muscle scars (Pl. 4, Fig. 7).

Some of the storm beds contain articulated bivalves, oriented with the plane of commissure sub-parallel to bedding. In some specimens one valve is laterally displaced 1 or 2 cm past the other (Pl. 4, Figs 4, 5). Pl. 2, Fig. 2 shows that in individuals tilted to the right, the upper valve is laterally sheared to the right. In individuals tilted to the left, the upper valve is sheared to the left.

Some shells exhibit in-situ breakage, apparently caused by compaction (Pl. 4, Fig. 6).

Discussion. — All observations on shell dissolution are in accordance with a laboratory experiment carried out by FLESSA & BROWN (1983). They studied dissolution rates in acid baths of 16 common species of the Bahia la Choya intertidal and shallow subtidal environments. They found that dissolution rates depended on size, mineralogy, and surface area to weight ratio and observed identical patterns of hard-part dissolution. However, some differences between laboratory experiments and field observations exist, showing the limitations of the former. For example, while calcitic barnacle plates dissolved most rapidly in the experiment, they are preserved as skeletons in the field, even where all other species are mainly preserved as molds and casts. This demonstrates that also other factors such as shell structure and ornamentation, porosity, and organic content influence the rate of dissolution (see also ABERHAN 1987, FEIGE 1987).

The common occurrence of casts and molds shows that shell dissolution occurred after compaction and cementation. An extensive diagenetic bias of the faunal composition can therefore be excluded.

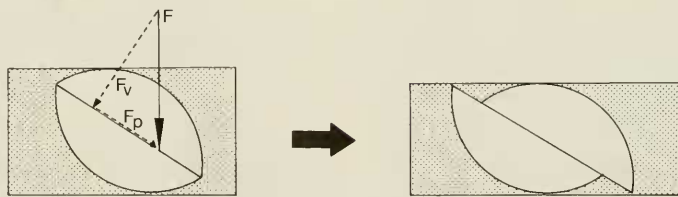


Fig. 6: Lateral shearing of valves of articulated bivalves can be explained by compaction. Prerequisite is burial of shells in a somewhat oblique position. With increasing burial the presence of overlying sediments produces shearing forces in the plane of commissure. The parallelogram of forces shows a force of compaction (F) that can be split in a component F_v vertical to the plane of commissure and a component F_p parallel to the plane of commissure. F_p is responsible for the lateral shearing.

The lateral shearing of shells is a taphonomic feature caused by compaction (Fig. 6): Articulated bivalves buried in a somewhat oblique position were exposed to shearing-forces in the plane of commissure caused by the pressure of overlying sediments.

TAPHONOMY: CONCLUDING REMARKS

As demonstrated above, a taphonomic analysis can provide useful information on rates of net sedimentation, rate of burial of shells, the energy level, and the degree of physical and

biological reworking in shallow marine environments. For the majority of the samples, taphonomic parameters could be correlated with different modes of shell bed formation.

Shells were concentrated mainly by a combination of low sedimentation rates and storm events. However, storm beds were modified by repeated reworking, resulting in a lowered degree of articulation and increased levels of boring and encrustation. Thus the original taphonomic characteristics can be completely altered. For example, an original storm bed reworked by successive storm events may no longer exhibit taphonomic features typical of storm deposits.

The ratios of articulated to disarticulated shells, of bored to non-bored and encrusted to non-encrusted shells can serve as indicators for the relative importance of storm influence and low sedimentation rate, and help in assessing the degree of reworking.

Due to subsequent modification, the Pleistocene deposits of Bahía la Choya do not show the couplets typical of temperate sites (e. g. KELLING & MULLIN 1975, AIGNER 1985).

Despite low rates of sedimentation and intermittent high energy conditions, lateral mixing of fauna was not significant; the Pleistocene deposits can therefore be regarded as parautochthonous. In contrast, temporal mixing of shells ("time-averaging" of WALKER & BAMBACH 1971), caused by low rates of net sedimentation, played an important role in shaping the

Pleistocene shell beds. The paleoecological implications of these time-averaged assemblages, in which parts of populations or communities that were living at different times are found together, will be discussed below.

In general, very few Pleistocene shells are encrusted, although many shells are bored. This is not due to preferred diagenetic dissolution of encrusting organisms, as is demonstrated by the high degree of encrustation at locality 6. A comparison with the distribution of encrusters in Recent intertidal and shallow subtidal habitats of Bahía la Choya shows that the environment is principally suitable for colonisation by encrusting organisms (Fürsich & Schödlbauer, this volume). Compared to boring organisms, encrusters possibly require longer-term stable substrates for colonisation.

Taphonomic data of section 6 indicate a shallowing of the depositional environment. Because of the relative tectonic stability of the region for the last 100,000 years (ORTLIEB 1977) and a sea level high stand during time of deposition (ORTLIEB 1984b), shallowing was the result of a regression. Thus, taphonomic studies may help to recognize transgressive and regressive cycles in fossiliferous depositional sequences. Such studies are particularly important when other facies characteristics such as grain size distribution, physical and biological sedimentary structures, geometry of deposits, or ecological features of fossils do not lead to an unequivocal interpretation.

PALEOECOLOGY

The taphonomic analysis indicates that the Pleistocene deposits are parautochthonous. Extensive biostratigraphic and diagenetic bias of the preservable part of the fauna can be excluded. The fossil associations are time-averaged and therefore do not reflect short-term conditions of faunal composition and diversity. However, time-averaged assemblages record long-term conditions of the depositional environment.

In the following section the environment of the Pleistocene fossil assemblages is reconstructed based on their taxonomic composition, molluscan diversity, trophic structure, and substrate relations.

BENTHIC ASSOCIATIONS

Using taxonomic composition and relative abundance of species the assemblages of the 16 samples were grouped in five associations. Four of them are dominated by bivalves and gastropods, in the fifth, balanids are the most common faunal element. Data on the relative abundance of species (with an approximate evaluation of their biomass using size), trophic composition, life habits, and substrate adaptations are found in Figs 7–11.

Chione association A

The *Chione* association A is represented by five samples (3a–b, 4a–c) with 1077 individuals. It is dominated by in-

faunal, suspension-feeding bivalves (Fig. 7). 65 taxa have been identified. The number of molluscan taxa varies from 13 to 50, the evenness (*sensu* MACARTHUR 1972: 197) from 2.2 and 18.3 between samples. 0.5% of the shells were bored by carnivorous naticid gastropods. The sediment consists of poorly sorted coarse sandstone.

Chione association B

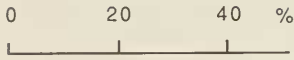
Three samples (1a–c) with 1604 individuals comprise the *Chione* association B. It is dominated by shallow and deep infaunal suspension-feeding bivalves (Fig. 8) and differs from the *Chione* association A largely by the rarity of the deep burrowing bivalve *Tagelus* sp.. 87 taxa have been identified; between 27 and 64 molluscan taxa occur in individual samples. Evenness values range from 1.3 to 15.9. Naticid gastropods bored 1.2% of the shells.

The sediment consists of poorly sorted coarse sandstone.

Balanid-vermetid association

All 5 samples from locality 6 with a total of 1288 individuals belong to this association. Balanids (*Tetraclita* sp. and *Balanus improvisus*) account for half the specimens. They colonize shells and cobbles alike (Fig. 9). Vermetid gastropods (*Tripsyche* and *Dendropoma*) are also very abundant, but due to their gregarious habit individuals could not be counted. They

Chione association A



Chione californiensis



Tagelus sp.



Trachycardium panamense

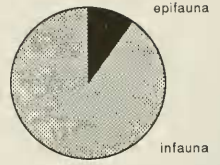


Neverita reclusiana

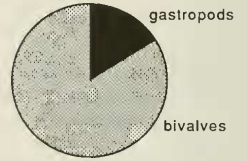
others



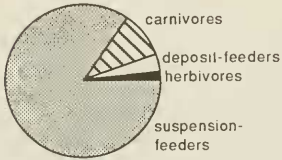
life habits



taxonomic composition



trophic composition



substrate adaptations

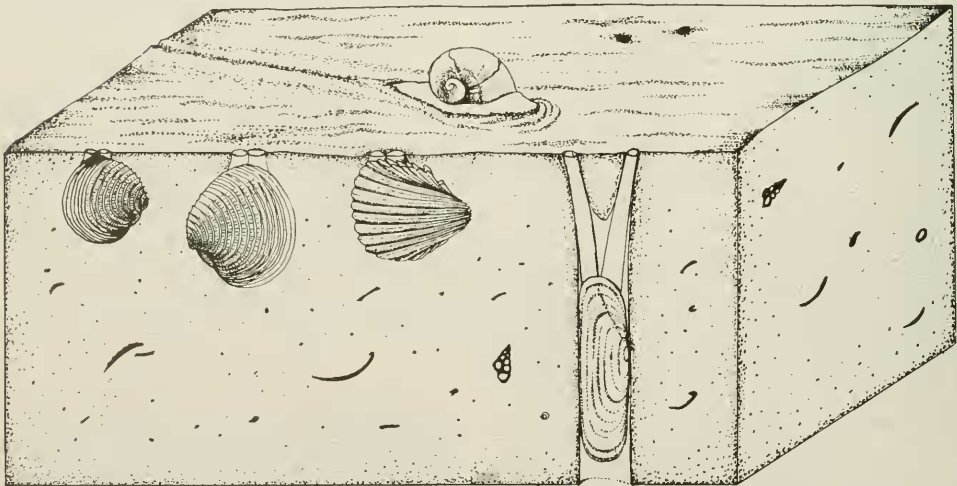
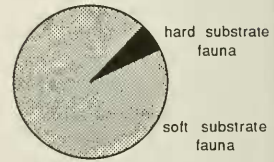
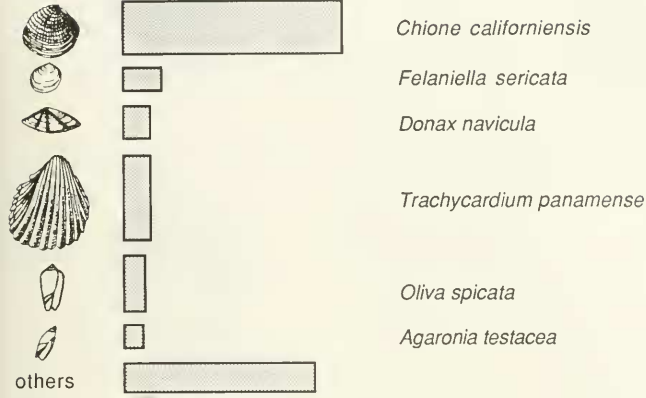
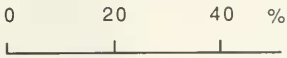
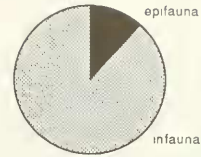


Fig. 7: Trophic nucleus, ecological features, and reconstruction of the *Chione* association A.

Chione association B



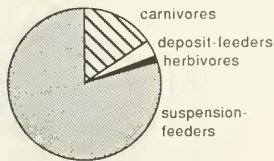
life habits



taxonomic composition



trophic composition



substrate adaptations

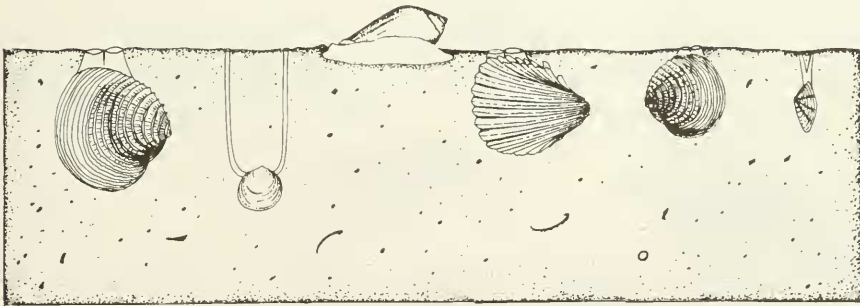
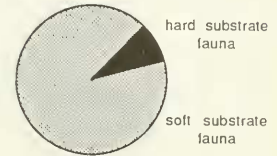


Fig. 8: Trophic nucleus, ecological features, and reconstruction of the *Chione* association B.

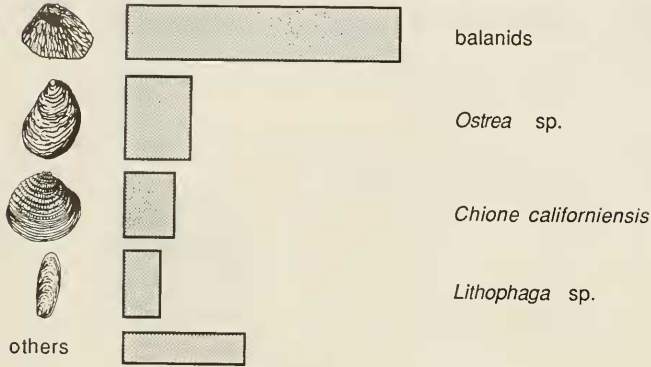
occur as lumps and are heavily bored by clionid sponges and *Litobopaga*. Next in abundance are cementing oysters and shallow infaunal bivalves. Crustose bryozoans increase in abundance up-section. Like vermetids, they could not be recorded quantitatively. 53 taxa were counted. The number of molluscan taxa in the different samples varies between 18 and 27; the evenness between 3.3 and 10.2. Only 0.2% of the

shells were bored by naticids. The sediment consists of, in places, densely packed cobbles and pebbles in a matrix of coarse sand and skeletal debris.

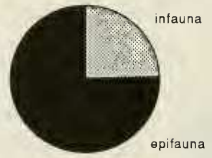
The five samples of locality 6 show an increase in the percentage of epifauna and hard substrate fauna up-section; the number of species remains roughly constant.

balanids-vermetids association

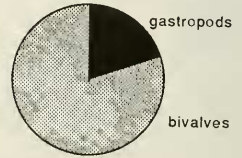
0 20 40 %



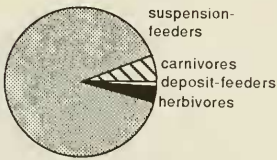
life habits



taxonomic composition



trophic composition



substrate adaptations

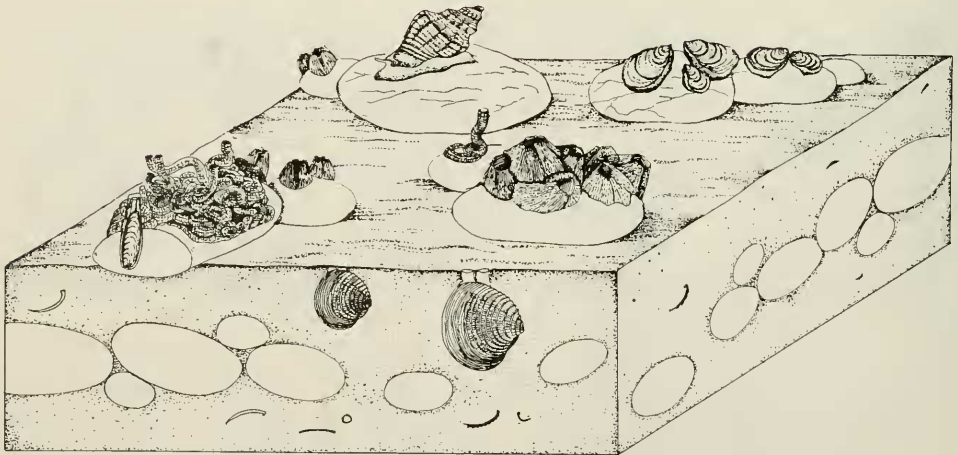
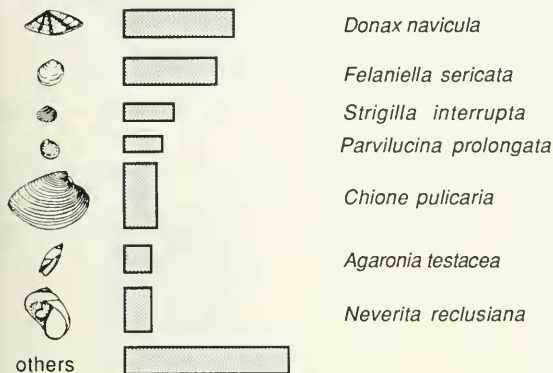
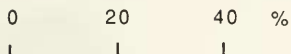
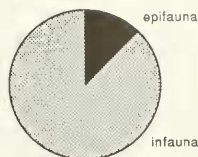


Fig. 9: Trophic nucleus, ecological features, and reconstruction of the balanid-vermetid association.

Donax-Felaniella association



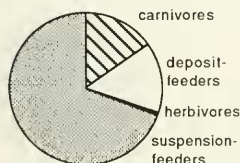
life habits



taxonomic composition



trophic composition



substrate adaptations

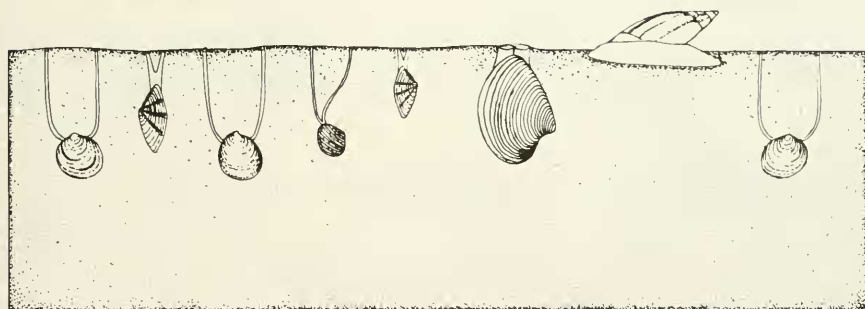
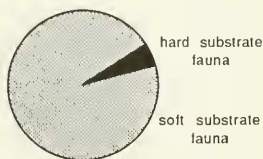


Fig. 10: Trophic nucleus, ecological features, and reconstruction of the *Donax-Felaniella* association.

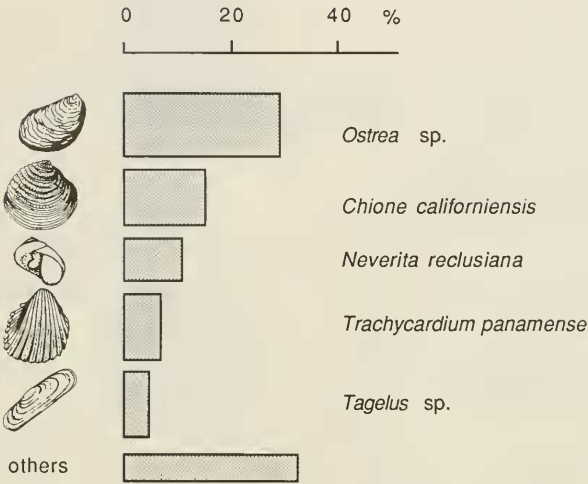
Donax-Felaniella association

Both samples of locality 2, with a total of 444 individuals, belong to this association. It is dominated by relatively small infaunal suspension-feeding bivalves (Fig. 10). 48 taxa have been identified, 23 (sample 2a) and 40 (2b) of which are molluscs. Evenness values are 7.7 (2a) and 10.0 (2b). 7.4% of the individuals have been bored by naticids. The sediment consists of well sorted fine sand.

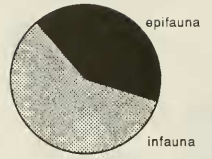
Ostrea-Chione association

The *Ostrea-Chione* association is represented by 196 individuals of the only sample at locality 5. The fauna consists of cementing oysters, infaunal bivalves and the naticid gastropod *Neverita* (Fig. 11). Of 39 taxa 37 are molluscs. Evenness is 8.2. 1.5% of the shells have been bored by naticids and muricids. The shells are found in a conglomeratic coarse sandstone.

Ostrea-Chione association



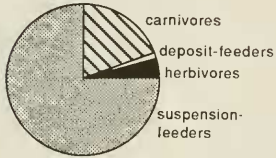
life habits



taxonomic composition



trophic composition



substrate adaptations

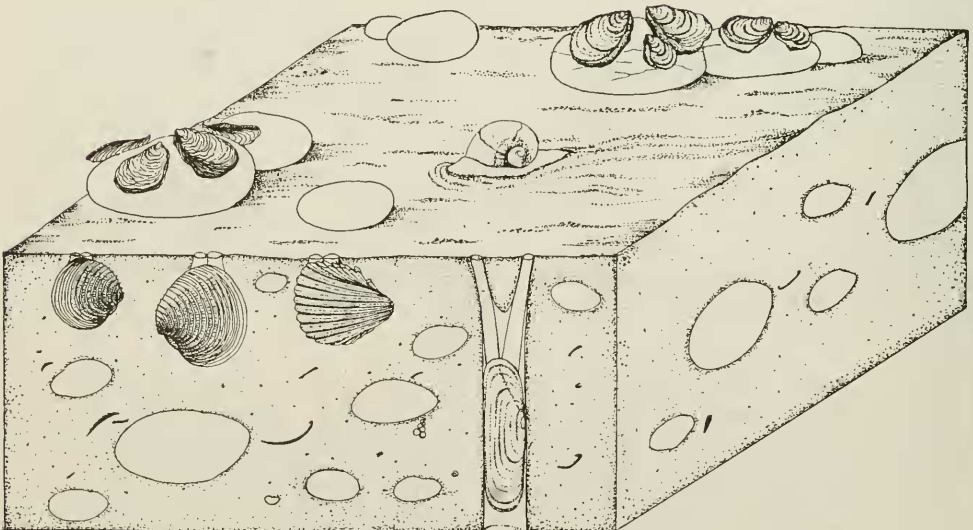
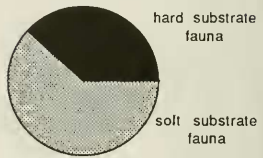


Fig. 11: Trophic nucleus, ecological features, and reconstruction of the *Ostrea-Chione* association.

DISCUSSION

Trophic and life habit groups

The fact that suspension-feeders strongly dominate all associations indicates that the energy level was sufficiently high to keep food particles in suspension. The dominant mode of feeding also reflects the coarse substrate in which organic matter is easily oxidized. Most faunal elements exhibit adaptations to a high energy environment where reworking is common. For example, infaunal bivalves are either thin-shelled deep burrowers (e. g. *Tagelus*, tellinids), thick-shelled shallow burrowers (e. g. *Chione*, *Trachycardium*, *Dosinia*, *Glycymeris*), or burrowed rapidly (e. g. *Tagelus*). Similarly, most epifaunal bivalves were thick-shelled and include byssally attached forms (e. g. *Arcopsis*, *Cardita*) or cementing taxa such as *Chama* and *Ostrea*.

Diversity and time-averaging

The diversity values of individual samples of the five associations vary considerably and cannot be interpreted meaningfully. This is true both of species richness (expressed by the number of species) and evenness (Fig. 12), whereby both aspects of diversity are positively correlated. Most likely this is a result of differing degrees of time-averaging to which the samples were exposed. Time-averaging increases the number of species (STAFF et al. 1986), whereas the evenness may or may not increase during this process. An increase in evenness during time-averaging results, for example, if the numerically dominant taxa have only a low fossilization potential or if the dominant taxa of successive populations differ due to environmental changes. In our Pleistocene samples changes in evenness appear to have been caused by changes in faunal composition as the fossilization potential of the dominant taxa is high.

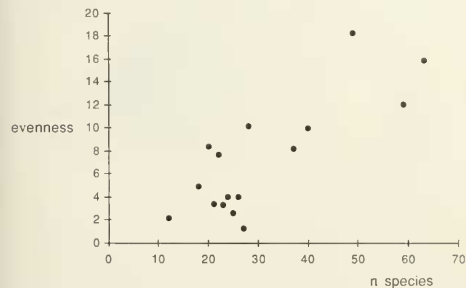


Fig. 12: Positive correlation of number of species with evenness. Dots denote individual samples.

The time involved in time-averaging of the Pleistocene faunas is not known. However, comparable molluscan death assemblages of the present-day tidal flat of Bahía la Choya show

similar values of number of species and evenness and have been proven to span a period of up to 4250 years (MELDAHL 1987). This time interval apparently is sufficient to produce the diversity figures observed in the Pleistocene samples. It cannot be determined, however, how rapidly diversity values increase by time-averaging and when a stable level is reached. In any case, time-averaging was long enough to obliterate any differences in diversity caused by possible habitat heterogeneity.

Changes in the diversity of taphocoenoses can also be a result of faunal mixing by transport. Evenness values in particular may be affected by selective dissolution of shells. However, as the taphonomic analysis has shown, neither of these processes had much effect on the diversity values of the Pleistocene samples.

Fauna-substrate relations

Substrate conditions exerted a major influence on the life habits, taxonomic composition, and relative abundance of species in the Pleistocene associations. For example, the balanid-vermetid and the *Ostrea-Chione* associations occur only in very coarse sediment where cobbles provided plenty of hard substrate for attachment. Infaunal species dominate in associations that occurred in sandy, mobile substrates (*Chione* associations, *Donax-Felaniella* association), whilst epifaunal species are most abundant in stable sediments with abundant cobbles (balanid-vermetid association). The *Ostrea-Chione* association occupies an intermediate position in terms of infaunal/epifaunal distribution because its substrate included both soft and hard sediments. These results are in good agreement with observations from the Recent (e. g. CRAIG & JONES 1966) and the fossil record (e. g. FURSICH 1976). In these studies the percentage of epifauna was related to the mean grain diameter of the substrate, whereas the Pleistocene associations of Bahía la Choya can be correlated with the maximum grain diameter.

A similar pattern emerges when the distribution of hard substrate fauna is plotted: the percentage increases with the abundance and maximum diameter of cobbles. This indicates that the fauna is autochthonous to parautochthonous (see FURSICH & SCHÖDLBAUER, this volume, for similar observation on the Recent tidal flat).

The trophic structure of the five associations is very similar (with suspension-feeders dominating) as only a portion of the total range of substrates is represented. The only association in which detritus-feeders are of some importance is the *Donax-Felaniella* association which occurs in well-sorted, fine sand.

All these observations suggest that the five associations represent remnants of physically controlled communities in which species interactions only played a minor role (see for example the low percentage of shells bored by predatory naticid gastropods).

DEPOSITIONAL ENVIRONMENT AND MODE OF FORMATION OF THE PLEISTOCENE SHELL BEDS

We use sedimentological, taphonomical, and ecological information to reconstruct the depositional environment of the Pleistocene. In addition, the Pleistocene faunas are compared with Recent faunas of the Bahía la Choya intertidal to shallow subtidal areas (for detailed information on the Recent fauna see FURSICH & SCHÖDLBAUER, this volume).

Reconstruction of substrate conditions is straightforward. Grain size indicates fine to coarse sandy substrates which differed in their degree of sorting, the amount of shell material and in the number of pebbles and cobbles. The lack of primary sedimentary structures points to intensive bioturbation which is also reflected by a number of well-defined burrow systems (e. g. Pl. 1, Figs 1, 6). In most cases apparently only the surface layer of sediment was mobile, whereas deeper layers were affected only by large reworking events. A relatively mobile substrate is indicated by the lack of epifauna (except where pebbles and boulders abound). The well-sorted fine sand in which the *Donax-Felaniella* association occurs prob-

ably represents the most mobile substrate. There species capable of rapid burrowing and deep burrowing are abundant. Densely packed cobbles, in contrast, colonized by cementing epifauna, indicate a relatively stable substrate. Substrate (mobility, consistency, and grain size) exerted the greatest influence on faunal distribution, whereas many other environmental parameters varied only little. For example, normal marine salinity and sufficient supply of nutrients and oxygen is indicated by the faunal composition, abundant infaunal elements, and by the lack of significant amounts of organic matter in the sediment.

The nature of the sediment is closely linked to the energy level. The sandy sediment mixed with shell debris points to a high (at least intermittently) energy regime. The large cobbles at locality 5 and 6 most likely formed in the surf zone at the foot of an alluvial fan. Taphonomic features of the shell beds demonstrate that reworking by storms played an important role, causing winnowing and concentration of hard parts.

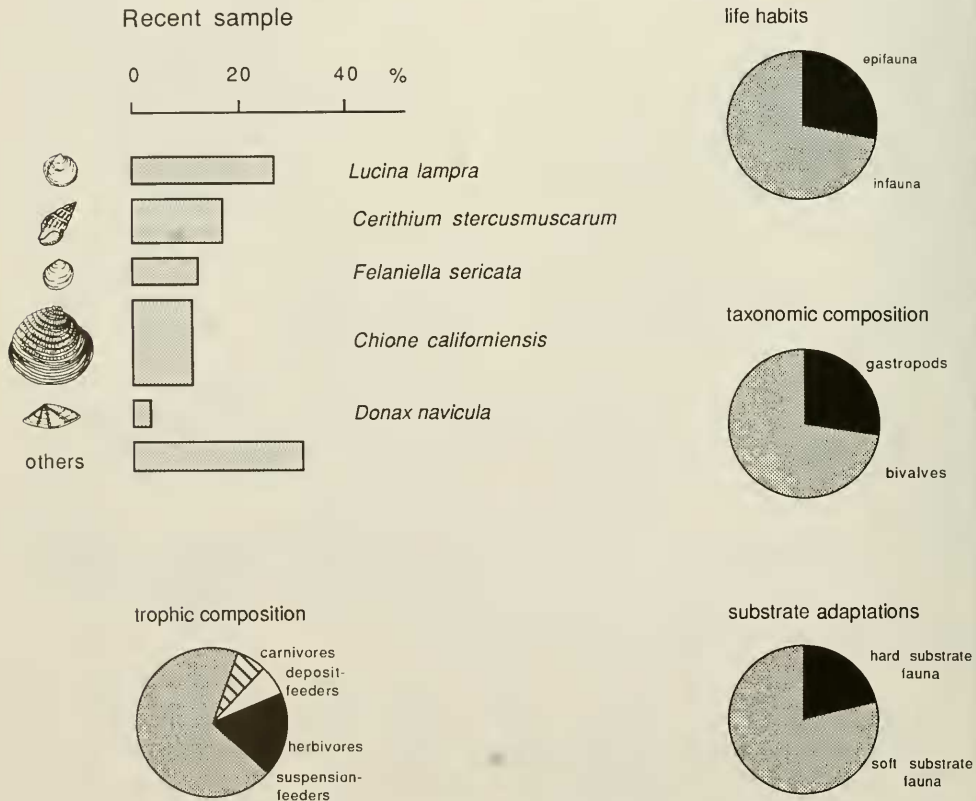


Fig. 13: Trophic nucleus and ecological features of sample from the Recent shallow subtidal.

Evidence for currents is less common and is best seen in the convex-up oriented shell bed of locality 2. Storm influence indicates deposition above storm wave base, whereas the presence of articulated bivalves not in life position suggests limited reworking. Deposition of the sandy sediments in the intertidal zone where constant reworking is taking place can therefore be excluded.

Additional evidence for the depositional environment of the Pleistocene can be gained by comparison with the taphocoenoses of the Recent intertidal flat and shallow subtidal of Bahia la Choya. All faunal elements of the Pleistocene have

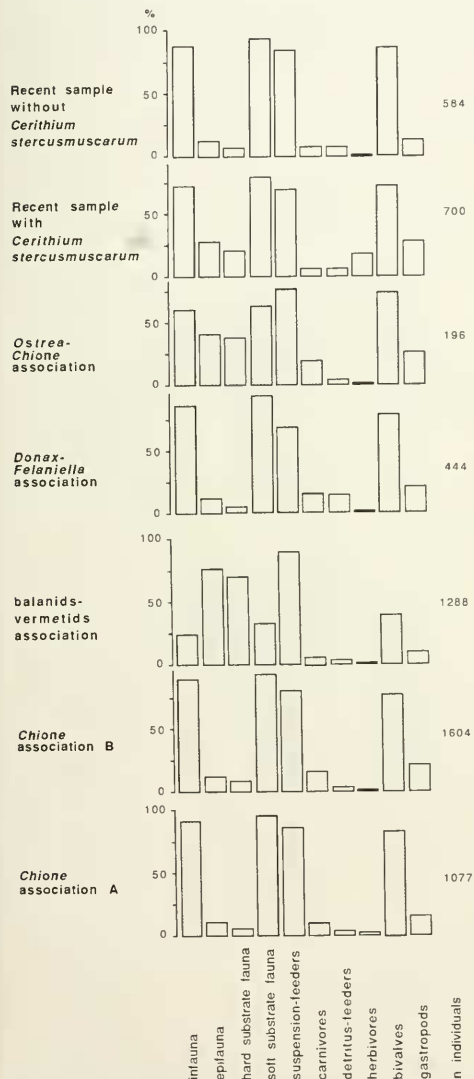


Fig. 14: Comparison of ecological data of the five Pleistocene associations with those of sample from the Recent shallow subtidal.

been recorded from Recent sandy or rocky inter- to shallow subtidal areas at Bahia la Choya. None of the Recent taphocoenoses (see FLESSA & FURSICH, this volume) exactly corresponds in faunal composition to any of the Pleistocene associations. The *Chione* and *Donax-Felaniella* associations are closest in composition to a sample from troughs of sand waves situated at the spring low water level (Figs 13, 14). *Felaniella sericata*, *Chione californiensis*, and/or *Donax navicula* are common elements of these associations and the taphocoenosis respectively. (The abundance of *Cerithium stercusmuscarum* in the sample from the Recent is a consequence of the adjacent rocky substrate. This species should therefore be excluded from the analysis when samples from sandy substrates are compared.) A major difference between Pleistocene and Recent samples is the abundance of the bivalve *Lucina lampra* in the latter. This species has been interpreted as a possible opportunist, being rare in live communities at Bahia la Choya, but one of the most abundant elements of the taphocoenoses of the tidal flat (FLESSA & FURSICH, this volume). Its scarcity in the Pleistocene can be explained in two ways. Either the bloom of the opportunist is so rare, that in the course of prolonged time-averaging its relative abundance is considerably reduced. Alternatively, *Lucina lampra* is an opportunist largely in the intertidal zone, but remains an inconspicuous element of the molluscan fauna in subtidal areas.

Some large species of the Pleistocene such as *Dosinia ponderosa*, *Trachycardium panamense*, and *Glycymeris gigantea* occur in the the Recent intertidal zone only as small juveniles. Large specimens are only found in the outermost troughs of sand waves of the outer flat and the shallow subtidal. This suggests a shallow subtidal origin of some of the Pleistocene faunas. The occurrence of two species of balanids encrusting cobbly substrates at locality 6 allows a fairly precise reconstruction of the water depth at that locality. In the lower part of the section, *Balanus improvisus* dominates, a species characteristic of the deep intertidal and subtidal zone (BRUSCA 1980: 212). In the upper part, *Tetraclita* sp. dominates over *Balanus* and is indicative of the higher mid-intertidal zone (BRUSCA 1980: 210). The sedimentological evidence of a shallowing upward sequence, indicated by the increase in the size of cobbles, is thus corroborated by the faunal evidence.

On the Recent tidal flat, detritus-feeders, largely gastropods, dominate inner flat firm substrates, whilst sandy mid to outer flats and subtidal areas are characterized by suspension-feeders, mainly bivalves (FURSICH & SCHODLBAUER, this volume). Because detritus-feeders are rare in the Pleistocene and bivalves dominate over gastropods, an inner flat environment can be excluded.

Recent intertidal sediments of Bahia la Choya consist of silty fine sand to medium sand. The Pleistocene sediments, in contrast, are predominantly coarse-grained and, in places, contain cobbles. A tidal flat environment thus is also unlikely from sedimentological evidence. A conspicuous feature of the Recent outer flat to shallow subtidal is the presence of large sand waves with accumulation of large shells in troughs, whilst the tops of the sand waves contain only sparse shell material of small size. At locality 1, a sequence occurs in which sediments grade twice from coarse sand containing abundant large shells upwards into poorly fossiliferous somewhat finer

sand (Fig. 2, Pl. 1, Fig. 3). This sequence may represent alternations of crest and trough environments of large sand waves comparable to those from the Recent. Again, this suggests an outermost intertidal to shallow subtidal environment for this Pleistocene locality.

In summary, sediments and faunas of the Pleistocene are

best interpreted as representing partly sandy, shallow subtidal environments, partly rocky shore environments. The latter are characterized by the balanid-vermetid and *Ostrea-Chione* associations, the former by the *Chione* and *Donax-Felaniella* associations (Fig. 15). True intertidal flat environments are not represented.

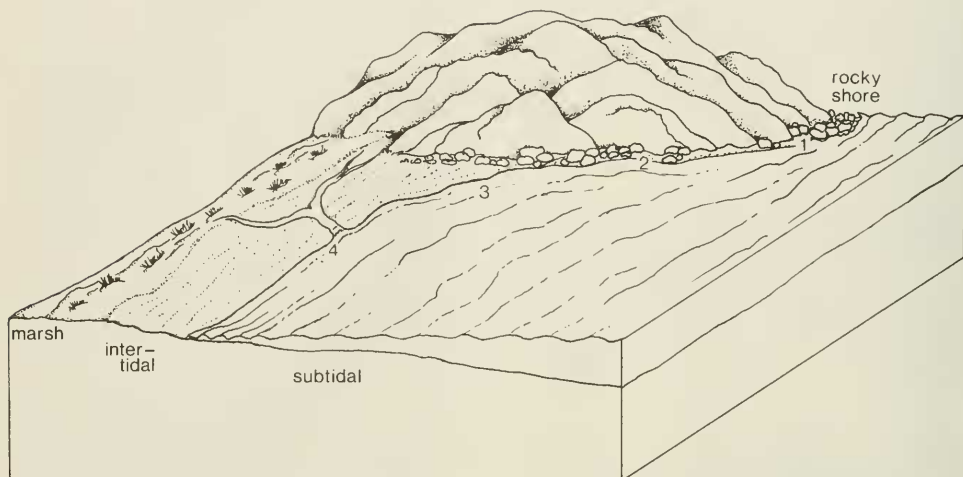


Fig. 15: Depositional environment of the Late Pleistocene benthic associations at Bahia la Choya. 1: balanid-vermetid association; 2: *Ostrea-Chione* association; 3: *Chione* associations; 4: *Donax-Felaniella* association.

CONCLUSIONS

- (1) Late Pleistocene (Sangamonian) rocks in the vicinity of Bahia la Choya consist of fossiliferous, fine- to coarse-grained sandstones and conglomerates.
- (2) The benthic fauna consists of 115 species and is dominated by bivalves (62) and gastropods (49 species). In addition, barnacles (2 species), scaphopods (1), and echinoids (1) occur.
- (3) The taphonomic analysis of shells showed that shell concentrations were caused by a combination of low sedimentation rates and storm events. Apparently, only small-scale transport of shells took place. As steinkern formation preceded dissolution of shell material, diagenetic distortion of the original faunal composition was insignificant.
- (4) The benthic fauna can be grouped in five associations which are related mainly to parameters of the substrate such as grain size, consistency, and mobility.
- (5) Due to differing degrees of time-averaging of the various shell concentrations, diversity values (both species richness and evenness) cannot be interpreted meaningfully.
- (6) Based on sedimentologic, taphonomic, and ecologic observations the Pleistocene rocks are thought to have formed partly in very shallow sandy subtidal areas, partly at a rocky shore. This conclusion is supported by a comparison of the Pleistocene faunas with those of the Recent tidal flat and shallow subtidal areas at Bahia la Choya.

ACKNOWLEDGEMENTS

We would like to thank ANDY FEIGF, KARL FLESSA, and SUSI SCHODLBAUER for assisting us in collecting the samples. We also acknowledge the hospitality of the Centro de Estudios de Desiertos y Océanos at Puerto Peñasco. The study was finan-

cially supported by a grant of the Deutsche Forschungsgemeinschaft (Fu 131/7-1). F. T. F. acknowledges a Feodor Lynen Fellowship of the Alexander von Humboldt Foundation at the University of Arizona in Tucson.

REFERENCES

- ABERHAN, M. (1987): Palökologie, Taphonomie und Ablagerungsraum spätpleistozäner Sedimente in der Umgebung von Bahía la Choya, nördlicher Golf von Kalifornien (Mexiko). – Unpublished Diploma-thesis, München.
- AGER, D. V. (1973): The nature of the stratigraphic record. – 114 pp., MacMillan, New York.
- AIGNER, T. (1982): Calcareous tempestites: storm dominated stratification in Upper Muschelkalk limestones (Middle Trias, SW-Germany). – In: EINSELE, G. & SEILACHER, A. (eds.): Cyclic and event stratification, 180–198, 9 figs, Springer-Verlag, Berlin – Heidelberg – New York.
- (1985): Storm depositional systems. Dynamic stratigraphy in modern and ancient shallow marine sequences. – Lecture Notes in Earth Sciences, 3, 174 pp., 83 figs, Springer-Verlag, Berlin.
- BECKVAR, N. (1986): Stratigraphy, taphonomy and fauna-substrate associations in a Gulf of California Pleistocene marine terrace near Punta Chueca, Sonora, Mexico. – 98 pp., 16 figs, Unpubl. M. Sc. thesis, University of Arizona.
- & KIDWELL, S. M. (1988): Hiatal shell concentrations, sequence analysis, and seal level history of a Pleistocene coastal alluvial fan, Punta Chueca, Sonora. – *Lethaia*, 21, 257–270, 8 figs, Oslo.
- BERNAT, N., GAVIN, C. & ORTLIEB, L. (1980): Datation de dépôts littoraux du dernier interglaciaire (Sangamon) sur la côte orientale du Golfe de Californie, Mexique. – *Bull. Soc. géol. France*, 12, 219–224, 1 fig., Paris.
- BRENCHLEY, P. J., NEWELL, G. & STANSTREET, J. G. (1979): A storm surge origin for sandstone beds in an epicontinental platform sequence, Ordovician, Norway. – *Sediment. Geol.*, 22, 185–217, 15 figs, Amsterdam.
- BRENNER, R. L. & DAVIES, D. K. (1973): Storm-generated coquinoid sandstone: genesis of high-energy marine sediments from the Upper Jurassic of Wyoming and Montana. – *Geol. Soc. Am. Bull.*, 84, 1685–1697, 14 figs, Boulder, Co.
- BRUSCA, R. C. (1980): Common intertidal invertebrates of the Gulf of California. – 513 pp., 14 pls, The University of Arizona Press, Tucson, Az. (2nd edit.)
- CLIFTON, H. E. (1971): Orientation of empty pelecypod shells and shell fragments in quiet water. – *J. Sediment. Petrol.*, 41, 671–682, 15 figs, Tulsa, Okla.
- CRAIG, G. Y. & JONES, N. S. (1966): Marine benthos, substrate and paleoecology. – *Palacontology*, 9, 30–38, 2 figs, London.
- DOIT, R. H., Jr. (1983): 1982 SEPM Presidential address: episodic sedimentation – How normal is average? How rare is rare? Does it matter? – *J. Sediment. Petrol.*, 53, 5–23, 20 figs, Tulsa, Okla.
- DURHAM, J. W. (1950): The 1940 E. W. Scripps cruise to the Gulf of California, part 3. Megascopic paleontology and marine stratigraphy. – *Geol. Soc. Am. Mem.*, 43, 1–216, Boulder, Co.
- EMERSON, W. K. (1960): Results of the Puritan-American Museum of Natural History expedition to western Mexico. 11. Pleistocene invertebrates from Cerralvo Island. – *Am. Mus. Novit.*, 1995, 1–6, 1 fig., New York.
- & HERTLEIN, L. G. (1964): Invertebrate megafossils of the Belvedere Expedition to the Gulf of California. – *Trans. San Diego Soc. Nat. Hist.*, 13, 333–368, 6 figs, San Diego, Ca.
- FEIGE, A. (1987): Taphonomie rezenter und pleistozäner Mollusken für die Rekonstruktion von Ablagerungsräumen (Bahía la Choya, nördlicher Golf von Kalifornien, Mexiko). – Unpublished Diploma thesis, Ludwig-Maximilians-University, München.
- FLESSA, K. W. & BROWN, T. J. (1983): Selective solution of macroinvertebrate calcareous hard parts: a laboratory study. – *Lethaia*, 16, 193–205, 10 figs, Oslo.
- & FÜRSCHE, F. T. (1991): Quantitative analyses of molluscan communities and taphocoenoses of Bahía la Choya (Gulf of California, Sonora, Mexico). – *Zitteliana*, 18, 79–88, 4 figs, München.
- FÜRSCHE, F. T. (1976): Fauna-substrate relationships in the Corallian of England and Normandy. – *Lethaia*, 9, 343–356, 7 figs, Oslo.
- & SCHOEDLBAUER, S. (1991a): Zonation of molluscan species across the tidal flats of Bahía la Choya (Gulf of California, Sonora, Mexico): Paleocological significance. – *Zitteliana*, 18, 53–70, 14 figs, München.
- & — (1991b): Zonation of molluscan life habit groups across the tidal flats of Bahía la Choya (Gulf of California, Sonora, Mexico): Paleoenvironmental significance. – *Zitteliana*, 18, 71–78, 5 figs, München.
- HERTLEIN, L. G. (1957): Pliocene and Pleistocene fossils from the southern portion of the Gulf of California. – *Bull. South. Calif. Acad. Sci.*, 56, 57–75, 14 figs, San Francisco, Ca.
- & EMERSON, W. K. (1956): Marine Pleistocene invertebrates from near Puerto Peñasco, Sonora, Mexico. – *Trans. San Diego Soc. Nat. Hist.*, 12, 154–176, 2 figs, San Diego.
- & — (1959): Results of the Puritan-American Museum of Natural History expedition to western Mexico. 5. Pliocene and Pleistocene megafossils from the Tres Marias Islands. – *Am. Mus. Novit.*, 1940, 15 pp., 5 figs, New York.
- KEEN, A. M. (1971): Sea shells of Tropical West America. – 1064 pp., Stanford Univ. Press, Palo Alto, Ca. (2nd edit.)
- & COAN, E. (1976): "Sea Shells of Tropical West America": Additions and corrections to 1975. – *Western Soc. Malacol., Occas. Pap.*, 1, 80 pp., Pomona, Ca.
- KELLING, G. & MULLIN, P. R. (1975): Graded limestones and limestone quartzite couplets: possible storm-deposits from Moroccan Carboniferous. – *Sediment. Geol.*, 13, 161–190, 17 figs, Amsterdam.
- KIDWELL, S. M., FÜRSCHE, F. T. & AIGNER, T. (1986): Conceptual framework for the analysis and classification of fossil concentrations. – *Palaaios*, 1, 228–238, 5 figs, Tulsa, Okla.
- KREISA, R. D. (1981): Storm-generated sedimentary structures in the subtidal marine facies with examples from the Middle and Upper Ordovician of southwestern Virginia. – *J. Sediment. Petrol.*, 51, 823–848, 16 figs, Tulsa, Okla.
- & BAMBACH, R. K. (1982): The role of storm processes in generating shell beds in Paleozoic shelf environments. – In EINSELE, G. & SEILACHER, A. (eds.): Cyclic and event stratification, 200–207, 2 figs, Springer-Verlag, Berlin – Heidelberg – New York.
- MACARTHUR, R. H. (1972): Geographical ecology. – 269 pp., Harper & Row, New York.
- MELDAHL, K. H. (1987): Sedimentologic, stratigraphic, and taphonomic implications of biogenic stratification. – *Palaaios*, 2, 350–358, 6 figs, Tulsa, Okla.
- ORTLIEB, L. (1980): Neotectonics from marine terraces along the Gulf of California. – In MÖRNER, N. A. (ed.): Earth rheology, isostasy, and eustasy, 497–504, J. Wiley & Sons, New York.
- (1982): Geochronology of Pleistocene marine terraces in the Gulf of California region, Northwestern Mexico. – In: 11ème Congrès INQUA, Volume de résumés, 2, 229, Moscow.
- (1984a): Radiometric and amino acid dating of Late Pleistocene fossils in the Gulf of California area, Mexico: available results and problems of interpretation. – In Symposium on neotectonics and sea level variations in the Gulf of California area. Abstract volume, 133–134, Hermosillo.
- (1984b): Pleistocene high stands of sea level and vertical movements in the Gulf of California area. – In Symposium on neotectonics and sea level variations in the Gulf of California area. Abstract volume, 131–132, Hermosillo.
- SALAZAR-JIMENEZ, A., FREY, R. W. & HOWARD, J. D. (1982): Concavity orientations of bivalve shells in estuarine and nearshore shelf sediments, Georgia. – *J. Sediment. Petrol.*, 52, 565–586, 12 figs, Tulsa, Okla.
- SEILACHER, A. (1982): General remarks about event deposits. – In EINSELE, G. & SEILACHER, A. (eds.): Cyclic and event stratification, 161–174, 2 figs, Springer-Verlag, Berlin – Heidelberg – New York.

- STAFF, G., POWELL, E. N., STANTON, R. J., JR., POWELL, E. N. & CUMMINS, H. (1986): Time-averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas Bays., — *Geol. Soc. Am. Bull.*, **97**, 428–443, 14 figs, 2 pls, Boulder, Co.
- STUMP, T. E. (1975): Pleistocene molluscan paleoecology and community structure of the Puerto Libertad region, Sonora, Mexico. — *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, **17**, 177–226, 21 figs, Amsterdam.
- (1981): Some Pleistocene facies and faunas of coastal Sonora and Tiburon Island, Mexico. — In ORTLIEB, L. & ROLDAN, J. Q. (eds.): *Geology of Northwestern Mexico and Southern Arizona*, 125–136, Univ. Nac. Aut. Mex. Inst. Geol., Hermosillo.
- THOMSON, D. A., MEAD, A. R., SCHREIBER, J. R., JR., HUNTER, J. A., SAVAGE, W. F. & RINNE, W. W. (1969): *Environmental impact of Brine effluents on Gulf of California*. — U. S. Dept. of the Interior, Res. Developm. Progr. Rep. No. 387, 196pp., Washington, D. C.
- WALKER, K. R. & BAMBACH, R. K. (1971): The significance of fossil assemblages from fine-grained sediments: time-averaged communities. — *Geol. Soc. Am. Abs. Progr.*, **3**, 783–784, Boulder, Co.

Plate 1

- Fig. 1: Vertical shafts of *Tbalassinoides* burrow systems; locality 1, layer c.
 Fig. 2: Shell bed; locality 3, layer a.
 Fig. 3: Shell bed; locality 1, layers a–c. Note large, sheared bivalves in layer b.
 Fig. 4: Coarsening upward sequence; locality 6, layers d–f. Hammer for scale.
 Fig. 5: Cluster of *Ostrea* sp. encrusting granite cobble; locality 6, layer e.
 Fig. 6: Horizontal *Tbalassinoides*; locality 4, layer d.

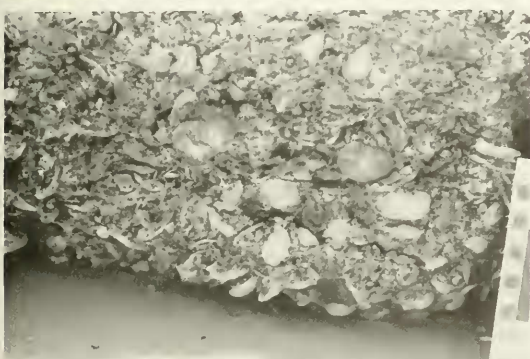
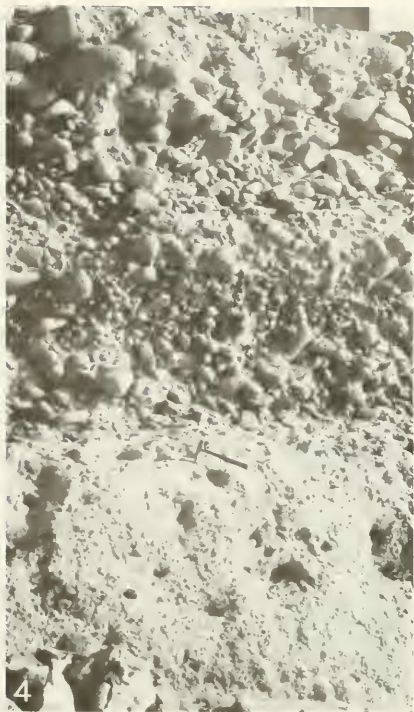


Plate 2

- Fig. 1: Acetate peel of bioclastic sandstone; locality 1, layer c; $\times 5$.
- Fig. 2: Laterally sheared bivalves (*Dosima*, *Laevicardium*, *Glycymeris*); locality 1, layers a–c. Hammer for scale.
- Fig. 3: Cluster of vermetid gastropods preserved as internal molds and heavily bored by clionid sponges and *Lithophaga* (arrowed); locality 6; $\times 2$.
- Fig. 4: Recrystallized gastropod shell with micrite envelopes; locality 1, layer c; $\times 20$.
- Fig. 5: Several generations of fibrous cement A (A) on shell (S). Larger voids are filled with blocky calcite (B). Quartz grains and smaller bioclasts are bound by micrite cement (C); locality 4, layer c; thin-section, $\times 20$.

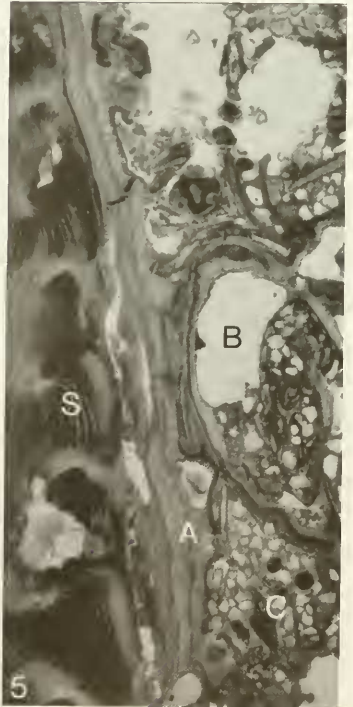
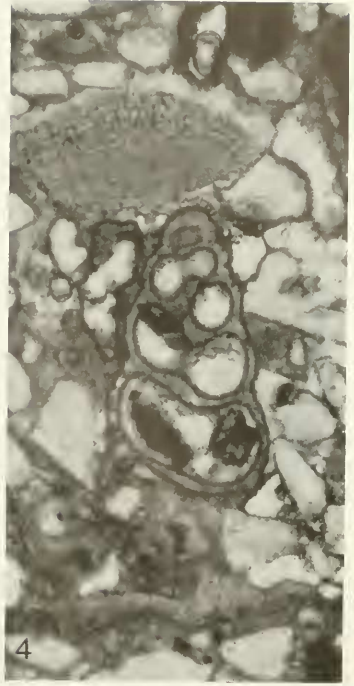


Plate 3

- Fig. 1: Comparison of maximum size of common bivalves from samples 2 a (right) and 2 b (left) of the *Dognax-Felaniella* association; locality 2; $\times 0.5$. (BSP 1990 XI 82-96)
- Fig. 2: Preservation of clionid borings: internal molds, shell dissolved (left) (BSP 1990 XI 97); unfilled borings (right) (BSP 1990 XI 98); $\times 1$.
- Fig. 3: *Chama* shell bored by clionid sponges and *Lithobaga*, the borings of the latter with calcareous linings (a). Encrusters are vermetid gastropods (b) and balanids (c). Locality 6, layer e (BSP 1990 XI 99).
- Fig. 4: *Neorapana tuberculata* encrusted by balanids; locality 6, layer e; $\times 1$ (BSP 1990 XI 100).
- Fig. 5: Borings of clionid sponges preserved as internal molds on a steinkern of *Turritella* sp., $\times 1$ (BSP 1990 XI 101).
- Fig. 6: Borings of *Polydora* sp. in shell of *Chione californiensis*; $\times 3$ (BSP 1990 XI 102).
- Fig. 7: *Melongena patula* bored by *Lithobaga* (a) and *Polydora* (b). Locality 2, layer b; $\times 0.5$ (BSP 1990 XI 103).



Plate 4

- Fig. 1: Size dependant dissolution of shells of *Chione californiensis*. Small individuals occur as internal molds, whilst large individuals exhibit original shell material. Locality 1, layer a; $\times 1$ (BSP 1990 XI 104–108).
- Fig. 2: Different modes of preservation of gastropods. Left: *Neverita reclusiana* with chalky texture; right: columella, often the part of shell which is most resistant to dissolution and commonly is still surrounded by steinkern (middle). Locality 6; $\times 0.5$ (BSP 1990 XI 109–111).
- Fig. 3: Thinning of the distal margin and accentuation of pre-existing shell sculpture in *Trachycardium panamense*. $\times 3$ (BSP 1990 XI 112).
- Figs. 4, 5: Laterally sheared valves of *Dosinia ponderosa* (4) and *Glycymeris gigantea* (5). 4: locality 2, layer b; $\times 1.5$ (BSP 1990 XI 113); 5: locality 1, layer c; $\times 0.8$ (BSP 1990 XI 114).
- Fig. 6: Compaction-induced breakage of *Tagelus* sp. (top) and *Chione* sp. (middle, bottom). Locality 3 (top) and locality 5 (middle, bottom). $\times 1$ (BSP 1990 XI 115–117).
- Fig. 7: Preferential dissolution of muscle scars in *Chione* sp.. $\times 1$ (BSP 1990 XI 118–120)

